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OBSERVATIONS ON THE GRYLLIDÆ: IV. COPULATION, *W. J. Baumgartner.*

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OBSERVATIONS ON THE GRYLLIDÆ: IV. COPULATION.

BY W. J. BAUMGARTNER.

(Contribution from the Zoölogical Laboratory, No. 196.)

Plate LXIV.

HISTORICAL NOTE.

THE first suggestion of the correct method of the transfer of the spermatozoa from the male to the female in the Gryllidæ is given by Siebold (*20*), who described the glands annexed to the ejaculatory duct and noted that their secretion coagulated very readily when exposed to the air, and that it probably served to fill and distend the copulatory pouch just as it filled and distended the penis. The latter organ surrounded a portion of the sperm and thus formed the spermatophore. Siebold believed with the older naturalists that the spermatophore is the end of the penis broken off and often reformed.

Stein (*22*) by his careful investigations gave the correct idea of the spermatophore as a vesicle formed by the secretion of the annexed glands and used to carry the sperm. Siebold (*21*) accepted this correction and later defended it. But he studied mostly locustids, and so we do not know that this part of his notes concerned the gryllids; however, some of his work was done on *Gryllus*, and so the work must be mentioned in a review of the subject.

We do have a comparatively detailed description of the act or acts of copulation in the crickets as early as 1855 by a Frenchman, M. Charles Lespes (*11*). But the work was little known and then questioned by Milne-Edwards (*15*); so that

textbooks of to-day still disregard it, or quote it with a question mark. Since I shall use Lespes's work very freely in my own description, I shall not review it farther here. Suffice it to say that the observations are strikingly keen and correct for having been made so early, and they should long since have been inserted in our texts.

Leydig (*13*) in his fine work, dealing more with the histological side of the subject, says that in many invertebrates the accessory sex glands form a spermatophore.

Milne-Edwards (*15*), in 1870, said, speaking of the spermatophore mentioned by Stein and Siebold: "It is possible that it may exist in certain cases, but in other cases it is evident to me that the appendage in question was certainly a part of the penis." Of Lespes's statements he writes: "It does not seem to me sufficiently demonstrated that the so-called spermatophore is not the terminal part of the penis which in copulation is broken off and remains inserted in the female apparatus, as it does so often in the case of other insects."

Milne-Edwards's prominent position, no doubt, gave his work the preponderance, and so we find Lespes's work hardly ever quoted. To show how it was disregarded, let me quote from Girard, who wrote three large volumes on entomology. In 1873 (*7*) he said of the glands joined to the *vas deferens*, "They pour in a liquid to delay or modify the sperm." In the third volume, in 1885 (*8*), he repeated the above statement about delaying the sperm, and then adds, "or perhaps to give more activity to the sperm, which are almost immotile in the testis."

Berlese (*4*) studied the external and internal genital organs of various orthopteran species. In the body of his work he does not seem to realize that the Gryllidæ differ from the other Orthoptera, and so he describes in *Gryllus* a penis and all the other accessory parts, without any thought of their correct function. In an appended "Physiological Note" he comes nearer the truth. He says, concerning copulation, that fertilization is internal and that copulation in the Acrididæ and perhaps in the Mantidæ is by means of a penis, the act lasting a relatively long time; while in the Locustidæ and Gryllidæ, "the male mounts on the back of the female, the penis being inserted in the vagina and the sperm injected in a short time."

He supposes that the mucus secretion of the annexed glands serves to lubricate the organs. He notes the fact that in *Gryllus* and *Gryllotalpa* the mucous secretion flows out through the same duct with the sperm. He adds further: "In *Gryllus*, I think, fecundation is more complex, occurring by means of a special organ which is left in the vagina of the female and which can be reformed up to three times a day, as I myself have seen. This singular organ holds the sperm in its interior and is a true spermatophore." The only way I can explain how Berlese came to overlook the discrepancy between his description and his "Physiological Note" is to think that in the body of the paper he was concerned with the homology of the parts in the various groups of Orthoptera, and so did not think of the function.

Graber (*9*) shows that in many Orthoptera there is no true copulation, but that the sperm are transferred by spermatophores. Palmen (*17*) studied by means of dissection and sections several species of Orthoptera, and he confirms Graber, showing the absence of a penis and the correct method of spermatozoon transfer.

Peytoureau (*19*) in his long thesis on the "Morphology of the Genital Armature of Insects," does not even mention Lespes's work, again showing how little this early, accurate investigation is known; or if known, how little it is appreciated. Peytoureau worked on the mole crickets, some long-horned and some short-horned grasshoppers. His special study was the hard parts, and he showed that the penis is absent, except in the Acrididæ, the Forficulidæ and the Ephemeridæ. But his study was centered about the homology of the male and female hard parts. Questions of the number of abdominal segments, the relative position of the ovipositor and the penis and to what segments these belonged, were the ones which he considered; and so the only observation of importance bearing upon our topic is the absence of the penis in the Gryllidæ.

Fenard (*6*) in 1896 published a long paper on "Les Organes Complimentaries Internes de L'appariel Genital des Orthoptères." He studied both sections and dissections of the annexed glands in the two sexes of several genera of most of the families of Orthoptera. In his observations he is correct on the whole. But in his interpretations he is not always so fortunate. The errors made are due largely to the fact, I

think, that he worked with preserved specimens only, and so missed the function of parts as proven by the habits of the animals. The suggestion that the anal gland in the mole crickets secretes a lubricant for the genital organs is entirely wrong, as I have shown elsewhere (*2*). Concerning the glands annexed to the ejaculatory duct he reasons correctly, as follows: Gryllids and locustids form a spermatophore, as shown by Siebold (*21*), Lespes (*11*) and Berlese (*4*). But these families are the ones that have this mass of annexed glands; hence these glands secrete the substance for the spermatophore. He thinks there must be a spermatophore formed in *Gryllotalpa*, although it has never been seen because of the habits of these insects. In this surmising he was fortunate, as I show below. But he is mistaken in the function of what he calls the ear-shaped gland. He thinks that it is analogous to the anal gland of *Gryllotalpa*. This is surely wrong. The position of the pair of glands and its relation to the excretory duct is such that it can have no such function as I have found for the anal glands of the mole crickets. My many dissections and observations lead me to believe that there is no gland which secretes a lubricant for the sexual organs.

Although the method of copulation by spermatophore and the function of the annexed glands have been so well described, it is rather disappointing to see our textbooks still quoting Carus's figures showing that the male generative apparatus of *Gryllus* is among the simplest found in the insects. See Henneguy (*10*) *et al.* Although this Frenchman cites Fenard's paper in his bibliography, he makes no reference to his findings, but says of the annexed glands: "Elles ont été peu étudiés jusqu' icé." But under the topic of "Copulation" he gives the process in *Gryllus* in detail, quoting Lespes's description and some of his figures of the spermatophore. In this case he does better than our own Packard (*18*), who, in speaking of the spermatophore, says: "In *Locusta*, and perhaps also in *Gryllus*, the sperm is enveloped by the secretion of the accessory glands of the seminal duct." This "perhaps" is very striking when one considers how easy it is for any one to observe copulation in our common field cricket. One need only catch an individual of each sex during the height of the breeding season, as indicated by their great chorus of chirping, and place them with a little grass over night or longer into

separate jars. Then slowly turn the glass with the male over that with the female. In a comparatively short time the male will begin his chirping and one can see the whole series of acts of courting and copulation. After observing the process one can hardly prevent a smile when he reads Loeb's (*14*) quotation of Yersin's experiment of having a pair of decapitated crickets copulate, and then see the admonition: "Of course it was necessary to place the male *on* the female." One would hope that the observations in the experiment itself, and any conclusions drawn therefrom, may be more to the point than is the self-evident suggestion added at the end.

DESCRIPTION.

A free translation of Lespes's paper of 1855 would describe fairly correctly and with a good deal of detail the various steps in the process of copulation. He notes at the beginning that there is no true copulation, but that the male simply deposits a spermatophore into the posterior end of the abdomen of the female; and that this process may be repeated many times.

The Courting.

Lespes (*11*) studied first the field cricket. Catching specimens of both sexes, he got them accustomed to their new surroundings and then brought the two together. "The male soon began to chirp, and to move around the female. Approaching nearer and continuing his chirping he turned his abdomen, carried very low, toward the head of the female. She remained quiet for ten minutes, not appearing to notice the maneuvers of her mate; then she moved forward a little and began to caress his abdomen with her mouth parts. Presently she mounted partly on his back; and he, stopping the chirping, glided back under her. The female vulva now rested above the end of the male abdomen."

This description of the courting is fairly exact. The caressing by the female is not essential or even usual. Sometimes the female hardly stops feeding during the whole process, simply allowing the male to slide under her. When the male approaches the female, or when she approaches him, his chirp becomes much softer and less shrill. On some occasions if the female did not yield after a certain amount of chirping the male became angry and fought his mate.

The Transfer of the Spermatophore.

Lespes says: "The plate, the tenth tergite, which covers the opening of the anus and the pieces of the genital armature, was raised, and a hook of this apparatus penetrated into the vulva. Immediately after this the end of a small brown body directed by the hook was introduced into this opening. The female then left the male, carrying the small brown body of which I have spoken." Lespes then removed the small apparatus from the female quite easily, as only its front end was inserted in the vulva. This apparatus he found composed of a small hard ampulla and a thin, transparent plate curiously twisted. Upon examining a jar in which he kept a male over night he discovered that there was a spermatophore lying on the bottom. He later proved that this was not exceptional, but that males deprived of females rid themselves of their spermatophores.

The male which had copulated with the female seemed exhausted and did not renew his courting for several hours, although he was again put in with the female. Lespes observed the transfer of the spermatophore very often, and each time he got a spermatophore from the female, which he studied later.

Taking up this transfer in detail, the Frenchman describes the position of the spermatophore in the male. "It lies in the posterior end of the abdomen covered by the supra-anal plate. To see it *in situ*, gently raise the anal plate which covers the anus; below this there is a horny plate with three hooks projecting backwards and upwards, and below this there is the spermatophore lying in the concavity of the eighth sternite. The ampulla extends backwards and is supported on either side by fleshy pallets (plate is used by Lespes). The plate and the thread of the apparatus are still in the organs which formed them. At the moment of copulation the supra-anal plate is raised and the hooks are introduced into the vulva, holding the two individuals firmly together. The end of the spermatophore plate from which projects the thread glides in a kind of hollow groove in behind the hook in a manner analogous to that which surgeons use when they introduce a bistoury upon a groove-director. By a rapid movement from before backwards the plate is fastened and the two pallets which hold the ampulla move aside, and so the spermatophore is carried by the

female, held by the plate only. Ten minutes after copulation some males had formed a new spermatophore, but it was soft and white, and attained its hardness and color only after an hour. The spermatophore can be quite readily removed from the male by means of a forceps. To form a new spermatophore the male goes through some motions similar to those used in defecation. The female carries the spermatophore for some time, in one case six hours, and it was not dropped until she mounted a male again."

My own observations show that this account is quite correct in most of the details. Our common black field cricket differs in the following points: The female if undisturbed will not leave the male immediately after the placing of the spermatophore. She may remain perfectly quiet for several minutes.

A third element of this sperm-bearer, which Lespes seems to consider of little importance, is very essential, as I shall prove below. It is the thread which projects beyond the plate. (See fig. I.) This thread slides in the groove when the apparatus is being introduced. The mechanical process can be better understood by examining figure 5. The ampulla lies between the two pallets, which are then extended backward very far. The plate lies in the anterior part of the mold and the thread lies in the groove below the hooks. In transferring the spermatophore the male turns the hooks upward by swinging them, or rather the whole mold, at its attachment to the tergite as a pivot. By this turning the hooks first extend upward and then forward and are thus inserted into the vulva of the female, holding her firmly. Then by means of the muscular mass behind, the thread and plate of the spermatophore are pushed far into the vulva. The hooks of the plate hold the apparatus and the thread carries the sperm into the spermatheca. The thread and the anterior end of the plate are quite flexible, and so they are bent and directed by the "independent piece with the short stylet" which guides the thread into the duct leading to the spermatheca. The "forward and backwards" movements are concerned with the proper placing of the thread.

The time suggested for a male to copulate a second time is much too long. I have had a second pairing occur in fifteen minutes. The spermatophore in this case was whiter and softer than usual, but as far as I could see it was a normal

copulation. This intervening time was unusually short, but I am sure that it does not take an hour for a spermatophore to harden after it is formed.

I am sure that the males of *our* field crickets rid themselves of the spermatophore, if deprived of the females, only *exceptionally*. In all my many observations I have seen the thing occur but three times, twice in *Gryllus* and once in *Nemobius*. In every case it was rubbed off after an unsuccessful attempt to introduce it into the female. In these trials the plate was, no doubt, partially removed from its normal position in the forming organs, because in most cases the males made no effort to remove the spermatophore, although they had tried to copulate.

I have not seen that the males make any movements while forming a spermatophore, but I would not positively deny that they do so. I have frequently kept them under observation for a few hours after copulation; some would form a new sperm bearer and others not. One male copulated a second time after a very short interval, but I did not watch him meanwhile. Some other specimens did not have the spermatophore formed after hours of watching.

The female carries the vesicle very frequently until she is about to mate again. If this comes soon after a previous copulation, she will remove the vesicle. She does this with her mouth parts, bending the abdomen ventrally. She may place herself partly on her back and holding the abdomen against the ground force her mouth parts back so as to reach the ampulla of the spermatophore. If the abdomen is too much distended by eggs, she frequently rubs it off by dragging the abdomen on the ground. The longer a spermatophore has been carried by the female the easier it is removed. In only one instance did I see a female mount upon a male with the sperm bearer still in place. After a good many efforts the male succeeded in pushing the old spermatophore partially out of the way and placing a new one. The female then carried both, the old one apparently hanging on by one hook.

The Spermatophore.

Lespes says: "The spermatophore of the field cricket is composed of a vesicle almost round, of a brown, more or less dark, color. It terminates at one extremity by a whitish papilla and is continued on the other end by a transparent plate, al-

most quadrilateral, formed by a thin membrane stretched over three small cartilaginous pieces. One of these is median and connects directly with the vesicle. It is tubular and contains a horny thread which continues well beyond the plate. The other two, situated to the right and left, are arch shaped, and their two ends covered by the membrane, form on either side two tooth-like hooks which serve to fix the apparatus in the vagina. The size of the spermatophore varies a little but ordinarily it attains almost 4 mm. from the papilla to the end of the plate. The thread appears longer or shorter according as it projects more or less from its tube. The spermatophore is of different consistency in different parts. The vesicle is extremely solid and its walls are very thick, while the plate and its cartilaginous thread are soft at the moment of copulation; besides, it is covered by a white, thick liquid which presents to me all the characteristics of a sperm fluid. The thick, hard vesicle, composed apparently of double walls, toward the extremities is hollowed out at the center. The roundish cavity is full of sperm. At one end a blind tube projects from the cavity into the ampulla. At the other end the cavity continues as a straight canal through the whole length of the plate. This canal contains the horny thread.

"The white liquid which covers the plate when first removed from the female shows, when examined with a high magnifier, a large number of small, thread-like zoösperms. They are about .04 mm. long and .002 mm. thick. These same bodies in great number fill the cavity of the vesicle. They were never united into feather-like bundles, nor did they ever show any movement. The fluid taken from the testis of the male or the copulating pouch of the female contains many very similar zoösperms. These never exhibited movement, however treated. Put into water, some of them twisted themselves into knots.

"When the female lets the spermatophore fall the walls of the vesicle are slightly ridged, but it still contains some sperm. The horny thread is no longer found in the tube of the plate."

I have quoted the above description at length because it gives many facts as I find them in our American species.

The vesicle and the plate are similar to those described above (see figs. 1 and 2). The thread is not contained in the tube, but it is the tube itself continued, and it is much longer, and bent back so as to run parallel with the plane of the plate

and vesicle (see fig. 1). It is a hollow tube for its whole length and the sperm comes out at the *end* of the thread, and not at the end of the plate, as Lespes supposed. The thread varies in length not because "it projects more or less from the tube" but because it is broken off in removing it from the insect. Many of those that I secured at first had more or less of the end broken off. It is easier to get a spermatophore with a complete thread from the male than from the female, especially if the latter has carried the apparatus for some time. This no doubt accounts for the fact that the apparatus can be more easily removed after it has been carried for a while. When the insect drops it normally the thread has been broken off, or, more probably, partly dissolved away; but it is not entirely gone, as Lespes states.

The vesicle is apparently double-walled as the Frenchman observes (figs. 1, 2, and 3). The inner one is thicker and more granular, while the outer one is harder and quite transparent (figs. 1 and 2). It is the inner wall that continues forward and forms the thread, although this substance is less granular than that around the vesicle. The substance forming the plate is somewhat granular, and in some cases took the stain just like the inner coat of the vesicle. In the lateral parts of the plates I saw in several of my preparations many vacuoles. The thread in many of the specimens fixed and mounted in balsam shows a tendency to break away from the plate (fig. 3).

That the sperm pass out at the end of the thread was nicely shown by several specimens which I placed into a normal salt solution. The sperm flowed out very regularly and moved about for a time. In one instance it took about fifteen minutes for a vesicle to empty itself through the end of the thread. After the sperm were all out a little fluid with small granules flowed out. I do not agree with Lespes when he says that some sperm remain in the vesicle normally; nor do I think that the wrinkling is a characteristic of the empty vesicle. I could not see any difference between an empty spermatophore and a dark brown one which had been carried by a male for some time. The wrinkling, which Lespes correctly describes, is due to the longer hardening of the vesicle and does not seem to affect the cavity on the inside.

The shape of the cavity differs from that described and figured by Lespes in the total absence of the blind tube extending into the papilla. What he describes is only the second layer

of the wall of the vesicle as shown in figures 1 to 3. The dark stain here shows the outer limits of the inner lining, and the cavity is on the inside, as shown in the outline drawings. The cavity is easily visible in the preparations but the photos do not bring it out. At the posterior end the cavity is flattened and at the other end it gradually tapers down to the size of the thread; so that the shape of the opening is much like a flat-bottomed flask. In this cavity all the sperm have their heads directed toward the openings into the thread and their tails toward the papilla. Figure 11 is a small group of sperm photographed from a section of a spermatophore. In passing out of the thread the sperm manifested some movement of their own, but were not very active. Several may pass out together but only two or three heads have room side by side. The sperm are larger than Lespes thought, as can be seen by comparing with my earlier published measurements (*1*).

The Spermatophore-forming Organ.

Since many of our textbooks on entomology—see Packard (*18*) and Henneguy (*10*)—still cite *Gryllus* as showing one of the simpler conditions for the excreting ducts of the testes among the insects, I shall give a more detailed account of the male generative organs, their ducts and the accessory glands, than I should otherwise do.

The first description of these parts was given by Dufour (*5*), in *Gryllus campestris*, then by Lespes (*11*), in *G. domesticus*, later by Berlese (*4*), again in *G. campestris*, and then by Fenard (*6*), in both of the above species.

The testes lie on either side of the abdomen above the alimentary canal and extend from the second to the sixth or seventh segments. The shape is much like that of an elongated strawberry. On the outside is a thin membrane which encloses the hundreds of straight or slightly curved tubules which make up the organ (figs. 6 and 7). Their blind ends are nearly all directed more toward the posterior end of the body of the animal. At the center of the testes is a large tube, or rather an irregular sinus, which receives the openings of the hundreds of tubules (fig. 8). The small *vas deferens* leaves this sinus on the anterior ventral side and comes to the ventral side of the testes a little back of the middle. It passes backward over the tubules, and leaving them at the outer posterior edge passes back along the body wall muscles till it reaches the

ninth segment, where it passes around the cercal nerve and a few strands of muscle and ligament (figs. 7 and 8). Making a sharp bend it goes forward and ventralward. It is very much coiled upon itself from the bend on (figs. 7 and 8). The loops of the coils may lie in planes passing dorso-ventrally or laterally. The two *vasa deferentia* join and immediately empty into the posterior ventral angle of the sinus, which receives the openings of the annexed glands (fig. 9). Beginning at the cercal nerve and sometimes a little in front of the bend the duct is swollen so as to be 0.5 to 0.75 mm. in diameter (figs. 7 and 8). Fenard says there are from four to five coils and that the total length is 8 mm. In our common field cricket I found no regularity about the position or number of coils and the total length is more than 10 mm.

This swollen part of the *vas deferens* is always in the mature adult filled with a mass of sperm, all of them with their heads turned away from the testis.

Fenard (*6*), as well as the older investigators, says that "the union of the two *vasa deferentia* forms the ejaculatory duct." This is the statement generally made of the insects higher in the scale of evolution; but it is true only in a certain sense—in the sense that it serves as a common duct to carry out the secretions of the testes. First, it is not a true ejaculatory duct in the sense that it "during coition conducts the sperm into the copulatory pouch of the female"—Packard (*18*). This is true only in those insects with a penis; but in the Gryllidæ, where there is a spermatophore formed there can be no such function. Second, nor is it true in the sense that it is formed by a growing together of the two *vasa deferentia.* It is formed by an invagination from the outside, as was first shown by Palmen (*17*) from the anatomical standpoint and by Nusbaum (*16*) from the embryological. This invagination projects quite far beyond the point at which the two *vasa deferentia* join it (fig. 7). It extends dorsalward and forward, where it receives the openings of the hundreds and hundreds of tubules of the annexed glands (fig. 9). The lumen is very much flattened laterally and widened vertically towards the blind end. The more muscular tube leaves the sinus at the posterior dorsal angle just above the point of entrance of the *vasa.* This is well shown in figure 9. The openings of the *vasa* cannot be recognized in this figure, but the serial sections leave no doubt as to its location.

The hundreds of glandular tubules which empty into the upper end of the common duct vary greatly in length and diameter, apparently depending in part upon the room they find for development (figs. 6, 7 and 9). They take up all the available space, completely surrounding the seminal vesicles, extending far backward beside the rectum and the spermatophore pouch, or crowding forward and upward around the intestinal tract. Many of them are short while others are long. The whole group of tubules forms a large mass which takes up quite a space (fig. 6).

The "prostatic gland," first noticed by Berlese and later described by Fenard, I found "only after much difficulty," as the latter says. From my dissections I had concluded that the part so described was a part of the irregular pouch which molds the plate of the spermatophore. But a careful study of serial sections reveals the presence of a pair of oval glands or pockets attached on either side to the common duct. They have very short connecting tubes and they lie in the muscular and connective tissue surrounding that part of the common duct between the ganglion and the mold. The glands are not surrounded by "yellowish fat," as Fenard suggested; but they have "thin walls and are filled with a clear fluid." This fluid seems to harden into a clear yellowish chitin-like substance when treated with fixatives. In this it resembles the secretion from the annexed glands; but their secretion is darker and more granular. Judging from the behavior of the secretion and the position and connections of these glands I think they do not furnish a lubricant, but probably have something to do with the formation of the more flexible thread and the plate.

The common duct, after passing close to the floor of the abdomen, turns dorsalward and then empties into the cavity of the spermatophore mold (fig. 9). This apparatus was carefully studied by Lespes (*11*). Many of his observations are keen and to the point, but his description in some points is not very clear. Berlese (*4*) studied this structure too, but he could not get away from the idea that he was dealing with the ordinary structures, so he applies the name "penis," etc., to the parts and so makes his description misleading. Fenard (*6*) pays no attention to the hard structures and so he does not make out the relations and functions of parts in this region. Peytoureau (*19*) studied mostly only the morphological rela-

tions of the hard parts and so he does not explain the functions of the parts of this organ.

Lespes describes this apparatus "charged with the formation of the spermatophore" as follows:

"It is situated at the posterior part of the ejaculatory duct and may be considered as a part of the genital armature. In the field cricket this armature is formed, first, by a curved plate composed of many pieces extending to the right and left and united by a tough membrane; and second, by a very remarkable independent inferior part. The plate itself is composed of six solid pieces. Above is a kind of shield-like piece which is easily divided along the median line. Posteriorly it ends in three hooks, of which the middle one plays an important part in copulation. To the right and left are long slender rods upon which are inserted the fleshy pallets which support the vesicle of the spermatophore. Below this shield are two others, thin and curved, with an irregular contour. Finally, on the inferior face of the dorsal shield are two small, slender plates. During copulation the median hook only enters the vagina and serves to conduct the plate of the spermatophore. The independent piece is formed in front by a sort of short stylet which is applied to the inferior face of the plate of which I have just spoken. At the base this stylet enlarges, changes its nature and forms a white plate with cross striations. This plate is bent along its length, forming an irregular circle. It is swollen into a very thin vesicle situated under the genital armature and in front of the two pallets which support the ampulla of the spermatophore. This pocket is largely open in front and under the genital armature. The ejaculatory duct, after having passed around the lower part of the spermatophore pouch, ends near this opening.

"This white plate is the organ for the production of the spermatophore. On its convex surface is a transparent line in which is formed the tube which holds the thread of the spermatophore. The size of the plate is greater at the two ends. At the terminal part of the enlarged inferior portion ends the ejaculatory duct."

Lespes claims to have seen the spermatophore while it was forming. "It had a very thin membrane. When completely formed the vesicle was removed out to the place between the two fleshy pallets, and the plate and the thread remained in

the forming organ, that is, in the stylet of the armature, until given off to the female."

This description is somewhat indefinite because of the uncertain meaning of the phrase "genital armature." Besides, the application of the words "in front" and "behind" is not certain. I do not believe that the differences between Lespes's description and my observations can be accounted for by supposing such differences exist in the different species studied. Both of us used *Gryllus domesticus* some, and as shown below we found only small minor differences between the house cricket and our own species of field crickets.

Before discussing the formation of this peculiar spermatophore farther let me state as clearly as possible the mechanical problem involved. There is a mold made up of a system of bracing rods of chitinous material and a thin fibro-muscular membrane. Into this mold leads a single tube, which has to bring the sperm and the secreted fluid for the covering. The ampullar part of the finished spermatophore has apparently a double wall, and so there may possibly be two kinds of secretions, although a careful study of the gland shown in figure 10 makes me doubt it. The question is, then: How are the sperm kept separate, and especially how are they *held* in the center while the soft liquid is poured around them and hardens? If there is a second layer in the wall the incomplete ampulla would have to be held in the center while the second inflow and hardening occurs. To place a semifluid substance within another fluid substance and hold the former at the center while the latter hardens would be a difficult feat for any mechanic. I do not see how the apparatus provided is sufficient to accomplish the result. Yet I have seen so many well-formed spermatophores that there can be no doubt of the end product.

The way to solve the problem readily suggests itself. One needs to get a lot of specimens showing the various stages in the formation of the vesicle. Such a series of stages I have been hoping to get, but have thus far not succeeded. In all my many dissections I have never found a partially formed vesicle. It is hardly feasible to follow the process in a living specimen, as the attempts to make observations would interfere with the normal formation.

Although I am not able to give a description of the exact method of formation, I shall nevertheless make some sugges-

tions. Lespes says that the ampulla is formed and then moved out to its position between the two pallets. I think that this cannot be correct, as it would mean that the plate and thread would have to be joined onto the ampulla. In all the specimens I have seen the inside cavity and the walls are just as smooth as they can be. I cannot imagine that if the apparatus is formed in two parts they could be joined together so exactly and smoothly. I would rather believe that the structure is formed as a whole *in situ*. The thing that gave the idea that it moved back is the fact that when the wall has partly hardened the pallets retract a little, exposing the ampulla.

When there is no spermatophore in a male cricket the hooks are drawn far down, the pallets are much contracted and folded, and a part of the loose tissue on the floor of the cavity is rolled up and fits into the mold as a sort of plug. The pallets and the plug have deeply grooved and ridged surfaces which line the small lumen within.

Things occur about as follows when a spermatophore is formed: The inner lumen becomes a little larger and assumes the shape of the cavity of the vesicle. Then the sperm pass down, filling it up. It is possible that the lining cells secrete a small amount of substance to form a thin membrane, and Lespes may have found an example in this stage. If a membrane is secreted it cannot be discerned later. Now some secretion comes down the common duct. This flows in and fills up the grooves. The ridges withdraw, forming new grooves to be filled up. The process continues till enough is laid down to form the inner layer of the wall. Then the flow ceases for a while, and the secretion hardens somewhat. After a longer or shorter time a second inflow of secretion occurs, and it takes the place of the withdrawn ridges till the surface of the lining membrane becomes smooth, thus forming the outer wall of the ampulla. Then the whole hardens into the completed spermatophore. I think the whole takes place in a short time relatively. There may be movements accompanying the process, although I have not observed them.

Since there is but one duct, the only other assumption which could be made is that the secretion and the sperm come down all together instead of in succession. If this be correct, then the long sperm would have to wiggle their way to the center. This is hardly possible. Besides, it would be difficult to explain the second layer in the wall of the ampulla by this hypothesis.

Another mechanical problem appears in the study of the spermatophore, namely, What causes the sperm fluid to flow out of the ampulla? Are they forced by contraction of the walls, or is there some substance that swells and forces them out? Does air penetrate the wall in some way and thus prevent a vacuum?

I do not believe that there is any contraction; at least not much. The walls do not collapse. Farther than this I could find nothing that would throw any light on the problem.

Differences Found in the Domestic Cricket.

Lespes describes the spermatophore and the spermatophore-forming organ of this species, but says that he has not seen the act of copulation. I can readily believe the latter statement, as the insects are much more shy and will not mate readily when watched. Nevertheless I witnessed the process several times. The behavior during courting and the movements during the transfer of the spermatophore are very similar to those of the field crickets. The differences are of no consequence.

The spermatophore is lighter in color, as Lespes says. But this is in accord with the general lack of color in this species. It is a little shorter and stouter, as the Frenchman indicated. The plate is also narrower and more bent. But the cavity does not extend back into the papilla, as I have already explained about our field crickets.

There is one point to which I should like to call attention. Lespes does not speak of it, yet shows a difference in the drawings. In the house cricket the thread is a direct continuation of the canal. This is correct for this species, and is precisely what I find in our field cricket. I have not seen the spermatophore in *G. campestris;* but judging from our domestic and field crickets, and the conditions I find in *Nemobius,* I do not believe that Lespes is correct when he indicates a break between the thread and the plate, as he shows in his drawings, figure 2. The canal could not be continuous if his drawing is correct. But Lespes thought that the thread was the mass of sperm, and so not thinking of the thread as a hollow conducting tube he might have a break in it.

The mold differs from that of our field cricket about as it differs from *Gryllus campestris,* judging from Lespes's description. The hooks on the superior plate are rudimentary or

absent, while the stylet is well developed and projects far backward. The cavity is smaller, making it necessary that the plate of the spermatophore be bent into a smaller curve. There are other minor differences in size and relations. Whether these differences are great enough to prevent intercrossing of species is not positively settled. I tried some experiments in cross-breeding, in which I was unable to get any cross matings; but the tests were not extensive enough to be very conclusive.

IN NEMOBIUS.

This genus resembles rather closely the form which Lespes describes under the name *Gryllus Sylvestris*. It is much smaller than our *Gryllus* and, like the European form, it likes the woods or shady places; in the grass under the trees of a park I have found the most specimens. In the months of August and September they are very numerous.

In its courting it is, like the domestic cricket, much more shy than the larger form, and it is rather tedious to watch till one catches a pair copulating. In the main the whole series of processes is quite similar to that in *Gryllus*. In the courting the male is more active while the female less readily yields to the courting. What Lespes (*12*) says of his forms holds true for our two genera: "Except some details of form and size all is similar. The spermatophore is smaller and more fragile but is similarly composed. The genital armature presents the same pieces, but they differ much in form." Lespes again in this species figures and describes the thread as continuous with the canal of the plate. This strengthens my belief that there is some mistake in the description of the spermatophore of *Gryllus campestris*.

I have succeeded in getting a good photograph (fig. 4), that shows the structure of the spermatophore of *Nemobius fasciatus*, our most common species, very well. The ampulla is almost a perfect sphere. Its wall is thick and its central cavity rather small and nearly spherical. As in *Gryllus sylvestris*, the plate is small and far from the ampulla, but the thread and plate are much more curved in our species (fig. 4). There is a fine, hollow, tube-like opening leading from the central cavity to the tip of the thread. There can be no doubt that the sperm fluid flows out through it.

IN GRYLLOTALPA.

Fenard (*6*) cites the fact that the Locustidæ and the Gryllidæ produce spermatophores and that those two families have the large mass of annexed glands. Continuing, he says: "Then wherever we find the glandular tubes similar to those in the above-mentioned groups we have a right to conclude, until there is proof to the contrary, that they secrete a substance destined for the formation of spermatophores more or less complex." He suggests that in *Gryllotalpa*, whose copulation has never been seen, fertilization occurs by means of a spermatophore, because they have the annexed glands similar to those of *Gryllus*.

In the abstract (*2*) I made the statement that in the mole crickets the sperm are transferred by means of a spermatophore. In order to observe copulation I kept four mole crickets, two pairs, for several weeks each in a separate aquarium partly filled with wet sand, grass roots and slices of potatoes. For five nights I placed them by pairs into battery jars which contained just enough sand to allow the animals to make a burrow around the edge. Thus I could watch them continuously. After some twenty hours I finally observed copulation. As a result of these vigils I am able to give the facts concerning chirping and the protective gland published elsewhere (*3*), as well as the following concerning copulation.

The courting is somewhat similar to that in *Gryllus*. The male calls the female with loud, long chirps. As she approaches the chirps become short and much softer. He then frequently turns his abdomen towards her. As the pair get ready to copulate the position assumed is quite different from that of any other animals of which I know. They turn posterior end to posterior end, and ventral side to ventral side, so that the cloacal openings are just opposite each other. The female stands erect with her abdomen slightly raised, while the male lies on his back. The abdomens are tightly held together by hooks, described with great detail by Peytoureau (*19*). The sperm were carried to the female by a spermatophore. The time it takes for the transfer is not over a minute; but the pair kept their relative position, the abdomens simply touching each other, for more than ten minutes. After disturbance the male followed the female and again assumed this

relative position, but no further transfer of a spermatophore occurred.

Right after the first separation of the couple the female began to chew at a part of the sperm vesicle, and only desisted when disturbed by the movements of the male. She was also perfectly quiet as soon as her abdomen was touched as in the position of copulation. One observation is not enough to establish the purpose of an act; yet, judging from the behavior of the individuals of this pair, especially from the anxiety of the male to touch the female with his abdomen, one could easily conclude that the long lying in the position of copulation was to prevent the female from chewing at the spermatophore too soon and thus preventing the proper injection of the sperm. After the pair had remained in the above-described position for ten minutes or more the female left the male and manifested no further desire to chew the spermatophore. She carried it for about a half an hour and then dropped it.

As the vesicle was being transferred, or just after it had been put in place, there was an outflow of some transparent fluid on either side of the vesicle. This soon hardened. It is this part of the apparatus that the female was chewing. The spermatophore was found to consist of an oval ampulla which contained the sperm in the cavity at the center. At one end of the ampulla there is a projection by which the apparatus is held in the vagina, and through which the sperm are carried into the spermatheca. On either side of this projection is an irregularly shaped mass formed by the above-mentioned outflowing fluid during the transfer. The two sides are unlike, as part of one side was pulled and eaten away by the female, and the other side was pressed out of shape by some falling sand before it had time to harden. Having but this one imperfect specimen of the spermatophore of these crickets I cannot give as accurate a description of its detail as I should like. Suffice it to say that it has the essential parts—a hollow ampulla to contain the sperm and a projecting part to fasten it to the female and to carry in the sperm. The structure of the latter is obscured by the irregular mass.

The outflow of this fluid recalls an observation which I made repeatedly in the Chicago greenhouses. In the copulation of a locustid the same phenomenon occurs, but in a more marked way. The species, an exotic one introduced from Japan, is

very abundant in the greenhouses. The male has no chirping organs and so the courting is all done by means of the long antennæ. The female mounts on the back of the male, when he hooks an almost spherical ampulla full of sperm into her vagina. During the latter act a viscid fluid flows out on either side and forms two somewhat irregular roundish masses larger than the original ampulla, which now lies between the two. Sometimes the female began immediately after copulation to eat this substance, doing it more readily if the couple was disturbed.

As to a use or meaning for this outflow of fluid and its subsequent hardening it is difficult to suggest a satisfactory one. Of its regular occurrence there can be no doubt, as I observed it many times in *Diastremmena* and once in *Gryllotalpa*. It may function as an additional fastener to hold the apparatus in the vagina. Yet this seems hardly necessary, as the spermatophore apparently remains in place before it is hardened. It may have something to do with the emptying of the vesicle, contracting around the ampulla, thus forcing out the sperm. Or it may be concerned with the removal of the spermatophore from the vagina, acting as a bait for the female to remove it.

SUMMARY.

1. The reproductive apparatus of *Gryllus* is not of the simplest type, as was reported by the earlier investigators and as is still suggested by our textbooks. These organs are rather of the most complex kind found among the insects. They were studied and described with a good deal of detail, and the correct method of the transfer of the spermatozoa was indicated by Lespes in 1855; but the work was discredited and neglected.

2. The male carries the sperm to the female in a special structure, the spermatophore, formed by the secretion of the glands annexed to the common duct.

3. The essentials of the spermatophore, as shown by the study of several genera of Gryllidæ, are a hollow vesicle to act as a retainer, and a hollow thread-like tube which carries the sperm into the spermatheca of the female. To the tube are added some enlargements which serve to hold the structure in the vagina.

4. The so-called genital armature of the male crickets consists of a mold for forming the spermatophore and an apparatus to transfer the same to the female.

5. The differences between the field and domestic crickets is probably great enough to prevent intermating, yet this is not at all proven.

6. *Gryllus* has no gland which secretes a lubricant for the copulatory organs. The so-called "prostatic gland" has to do with the formation of the thread and plate of the spermatophore.

7. Mole crickets form a spermatophore. A transparent viscid fluid flows out during the transfer. The male and the female assume a very peculiar position relative to one another during copulation.

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